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Survival rates of wild and released White-rumped Vultures *Gyps bengalensis*, and their implications for conservation of vultures in Nepal.

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Beginning in the mid-1990s, populations of three species of *Gyps* vultures declined by > 97% in South Asia in little more than a decade, caused by unintentional poisoning by the non-steroidal anti-inflammatory drug (NSAID) diclofenac. This led to a ban on the veterinary use of the drug, and establishment of conservation breeding programmes, throughout the region. Once much of Nepal had been confirmed as being free from diclofenac, beginning in 2017 White-rumped Vultures *Gyps*

bengalensis were released from the captive breeding population. A total of 99 birds (*n* = 50 wild and *n* = 49 released) were fit with GPS transmitters between 2017-2022 and monitored daily. Tag fixes suggesting death or ill-health were followed up and dead vultures retrieved for post-mortem analysis. The estimated annual survival of wild adult vultures was 0.974 (95% CI, 0.910-0.997), while that of wild subadults was 0.880 (0.721-0.966). Survival rates of released birds were lower than those of wild birds, being 0.644 (0.490-0.778) for adults and 0.758 (0.579-0.887) for subadults. Post-mortem analysis of dead vultures indicated several possible causes of death, including predation, infection and electrocution. There was no evidence that any birds died of NSAID poisoning. The high survival rates of wild birds, especially adults, and the lack of evidence for NSAID-caused mortality, suggest that vulture habitat in the Nepal VSZ is free from diclofenac and that other hazards are sufficiently infrequent to allow the vulture population to recover. The lower survival of released birds compared to their wild counterparts suggests a need to improve the conservation breeding programme and release protocol.

Keywords: GPS, satellite tracking, conservation breeding, captive-reared, captive-bred, non-steroidal anti-inflammatory drug (NSAID), mortality

Populations of three *Gyps* vulture species endemic to Asia underwent catastrophic declines between the mid-1990s and mid-2000s (Prakash *et al*. 2003, 2007; Pain *et al*. 2008). As a result, the Red List status of White-rumped Vulture *G. bengalensis*, Indian Vulture *G. indicus* and Slender-billed Vulture *G. tenuirostris* was changed from Least Concern to Critically Endangered in 2000 (Birdlife International 2021). The declines were caused by veterinary use of the non-steroidal anti-inflammatory drug (NSAID) diclofenac, which was used on a large scale in South Asia as a palliative treatment for sick and injured domesticated cattle (*Bos taurus, B. indicus* and *Bubalus bubalis*). Ingestion of a typical meal of tissue from cattle treated with diclofenac a few days before the animal's death caused vultures to die from kidney failure (Oaks *et al*. 2004, Green *et al*. 2006).

Numbers of these vultures in India were reduced by over 97%, and the population of the worst-affected species, the White-rumped Vulture, declined by 99.9% (Prakash *et al*. 2007). There were also large declines in the adjacent countries: Pakistan, Nepal and Bangladesh (Pain *et al*. 2008). This was equivalent to the loss of several million vultures in little more than a decade (Prakash *et al* 2017).

Following the identification of diclofenac as the cause of the rapid vulture declines, three recommendations were proposed to prevent the imminent extinction of *Gyps* vultures in south Asia: regulation of veterinary use to remove diclofenac from vulture food sources, identification of an alternative vulture-safe drug for cattle and the establishment of a conservation breeding programme (Bowden *et al*. 2012). In 2006, the governments of India, Pakistan and Nepal banned the manufacture, importation, and use of diclofenac for veterinary purposes, followed by Bangladesh in 2010. In 2005, experiments on captive *Gyps* vultures of several species showed that the NSAID meloxicam was safe to vultures at doses likely to be encountered by wild birds (Swan *et al*. 2006, Swarup *et al*. 2007). To promote the ban on diclofenac and its replacement with meloxicam, the concept of the Vulture Safe Zone (VSZ) was established (Mukherjee *et al*. 2014). A VSZ is an area of at least 30,000 km^2 centred on a breeding site of wild vultures. Its size was based upon estimates of home range size of adult White-rumped Vultures (Gilbert *et al*. 2007). The key idea behind VSZs is to allow conservation efforts to be focussed on a manageable area that is of ecological relevance to vultures (Mukherjee *et al*. 2014). Within a VSZ, local conservation teams run a programme of advocacy and education intended for local stakeholders, including state officials, veterinarians, para-veterinarians, pharmacists, and livestock owners. Its aims are to reduce the veterinary use of diclofenac and promote the use of safe alternative drugs (Mukherjee *et al*. 2014). Running parallel to this advocacy work, the prevalence of diclofenac (and other NSAIDs) is monitored by undercover surveys of products dispensed by veterinary pharmacies (Galligan *et al*. 2021) and analysis of NSAID residues in samples taken from cattle carcasses (Cuthbert *et al*. 2014).

Most VSZs have no legal status but are assessed by the international vulture conservation consortium, Saving Asia's Vultures from Extinction (SAVE: SAVE 2015-2021). In SAVE's assessments, all VSZs start out as *provisional* and are upgraded to full VSZ status only when the threat to vultures from diclofenac has been reduced to a low level. Ideally, this requires the fulfilment of several criteria. These include two years of monitoring showing that veterinary diclofenac is not being offered for sale in pharmacies and that no diclofenac residues are present in a minimum of 800 cattle carcass liver samples (Mukherjee *et al*. 2014). After at least five years of monitoring, no dead vultures should be found with symptoms of diclofenac poisoning and vulture populations should be stable or increasing. Undercover surveys of pharmacies are relatively easy to conduct (Galligan *et al*. 2021), but the other types of monitoring are difficult and expensive. In particular, given the current rarity of vultures in South Asia, very few are found dead and examined post mortem, so it is difficult to obtain unbiased estimates of the importance of different causes of mortality, including that by NSAID poisoning. Therefore, to establish whether poisoning by diclofenac (and other NSAIDs) is still an important cause of mortality, and to assess the safety of the VSZs, 50 wild vultures were fitted with GPS telemetry devices from 2017-2022 and intensively monitored (Mukherjee *et al*. 2014), combined with the rapid retrieval and post-mortem examination of carcasses of birds that die.

Anticipating the possible extinction of all three of these endemic Asian *Gyps* vultures in the wild, a conservation breeding programme was established to act as an insurance captive population and a source of birds to reintroduce into the wild once the threat from diclofenac had been removed (Bowden *et al*. 2012). In 2004, the first wild vultures were taken into captivity at the Vulture Conservation Breeding Centre at Pinjore, Haryana in India, which had been initially established to study and care for sick birds. Since then, nestlings of all three Critically Endangered vulture species have been collected from the wild and taken into captivity in India (Pain *et al*. 2008) and large numbers of birds have been bred, including second-generation young (SAVE 2015-2021). Additional conservation breeding centres have since been established in India, Pakistan and Nepal. In Nepal, 60 White-rumped Vultures were taken into captivity from 2008 to 2010, and the conservation breeding

centre in Chitwan National Park has produced a total of 19 fledglings (Bowden *et al*. 2012; SAVE 2015-2021). Recent surveys of pharmacies in the Nepal VSZ found very little veterinary diclofenac (Galligan *et al*. 2021), and road transect surveys indicated that wild populations of White-rumped and Slender-billed Vultures had ceased to decline and began to recover since about 2013 (Galligan *et al*. 2020). This suggested that the risk from diclofenac within the VSZ had been reduced to a low level and the decision was taken to release some of the vultures from the Chitwan conservation breeding centre (Bhusal *et al.* 2017).

To further check on the safety of the VSZ and the effectiveness of releasing captive vultures, all 49 White-rumped Vultures from the conservation breeding population have been released from captivity from 2017-2022 after being fitted with harness-mounted GPS transmitters. This included 34 birds that had been captive-reared and 15 that had been captive-bred. Captive-reared birds were originally taken into captivity as nestlings, from 2008-2010, and reared in captivity before being released as adults (10+years old). Captive-bred birds were hatched as part of the conservation breeding programme and released aged between 21-35 months. In this paper we report estimates of annual survival rates of wild and released birds and, where known, the cause of death of tagged birds.

Methods

A total of 50 wild White-rumped Vultures were trapped in a walk-in aviary (18 x 11 x 6 m) at Jatayu Restaurant, Kawasoti, Nawalparasi District (Fig. 1), baited with the carcass of an NSAID-free cow or water buffalo on six dates between April 2017 and March 2022 (Table S1). We classed birds at capture as adult (> 4 years old; n = 35) or subadult (< 4 years old; n = 15) using plumage characters validated using the appearance of known-age captive-bred birds. We released wild birds immediately after tagging. Captive birds were moved from the conservation breeding centre in Chitwan National Park to the release aviary at the Vulture Safe Feeding Site in Pithauli 3-7 months

before release. They were given a health check by a veterinarian a week before release, which included the analysis of blood and faecal samples, for presence of parasites. GPS transmitters were attached at this time. Birds were released on five dates between November 2017 and March 2022 (Table S1).

We marked each vulture individually, either with two numbered patagial wing tags (*n* = 61; Maquia Serveis Ambientals, Alicante, Spain) or, after 2020, with a numbered rivetted aluminium leg ring (*n* = 38; I.Ö. Mekaniska AB, Bankeryd, Sweden). We attached a GPS transmitter to each bird, and biometrics were taken. Tags were fitted with a thoracic X-strap harness with the tag resting on the bird's back (Orr-Ewing *et al*. 2020). Tags were either Solar Argos / GPS 30 g Platform Transmitter Terminal (PTT; *n* = 13 wild, *n* = 16 captive birds; Microwave Telemetry Inc, Columbia, Maryland, USA), which transmits data via the Argos satellite system or GPS-GSM transmitter (30g GSM-GPS OrniTrack-30s, Ornitela, Vilnius, Lithuania (n = 35 and n = 28), or 28g Telemetry Logger KITE-H LF GPS, Ecotone, Gdynia, Poland (*n* = 2 and *n* = 5)). Data transmitted from GPS-GSM tags was obtained via mobile phone connection and accessed from the Ornitela / Ecotone websites. Tags were programmed to collect 4-14 fixes per day between dawn and dusk, although the frequency was reduced to preserve battery power if voltages fell below certain levels. The maximum total weight of the transmitter, harness and wing tags / rings was 110 g, and constituted about 2.3% of body weight.

We monitored vultures feeding at the Jatayu restaurant to identify wing tags and rings opportunistically. Cattle carcasses known to be free from diclofenac were provided at the Jatayu Restaurant at least twice per week starting in 2017 and throughout the study. We monitored the data from the GPS transmitters daily. If GPS fixes suggested the bird was consistently stationary, or if accompanying accelerometer / battery voltage data suggested that the bird might have died, we travelled to the location and searched for it. Carcasses of birds found dead were retrieved and, if not too decomposed, taken to the National Trust for Nature Conservation-Biodiversity Conservation

149 Centre at Sauraha for post-mortem examination. Tissue samples were taken for further analysis of
150 possible cause of death.

151 *Statistical analysis*

152 We assumed that a bird whose tag had stopped transmitting and which was not seen alive
153 subsequently had died at the time when the tag was lost to follow-up, even if the bird's carcass was
154 never located. If a bird's tag stopped working, but the bird was subsequently seen alive, it was
155 assumed to have been alive and monitored up to the last day on which data transmissions were
156 received. The data were right-censored at that date (n = 5 wild birds). One of these wild birds was
157 found dead after being seen without its transmitter, which had fallen off, but its death and the days
158 between tag loss and death were not included in the analysis because it occurred after the period in
159 which it was being monitored. Some tagged released birds (n = 11) were found incapacitated by ill-
160 health, dehydration or starvation and were captured and taken into captivity for treatment. In the
161 survival analysis, we assumed that these birds had died on the date of capture, because this would
162 almost certainly have been the case without our intervention. Five of these recaptured individuals
163 recovered and were released again with a functioning transmitter, but data obtained after their
164 second release have not been included in the survival analysis. Our assumptions are 'worst case' in
165 that it is possible that some loss-to-follow-up events we took to represent deaths might have been
166 due to failure of the transmitter or shedding of the harness, with the bird not being detected
167 subsequently by visual observations. We based the date of suspected mortalities on the reduction in
168 battery voltage and temperature of the tag using data provided by the tag manufacturers.

169 Our analyses to estimate survival rates of tagged vultures during the periods over which they were
170 being monitored treated each day of monitoring as a binomial trial with a binary outcome: death or
171 survival. Statistical models of this type are often referred to as 'known-fate models' (see Chapter 16
172 of Cooch & White 2018). These methods allow for the fact that the death/survival outcome can only
173 be determined during the period of monitoring. Our initial analyses involved comparing daily

mortality rate (DMR) as m/d, where m is the number of deaths observed or inferred during monitoring and d is the number of bird-days over which birds were monitored and comparing the results across categories of birds and time periods (Table S2). We calculated annual survival rates (S) from the daily mortality rates as:

$S = (1 - \mathrm{DMR})^{365.25}$.

We calculated Clopper-Pearson exact binomial 95% confidence limits for DMR (Clopper & Pearson 1934) and used these limits to calculate confidence limits for S using the expression above. Although surviving birds continue to be monitored, the current analysis is confined to the period up to and including 8th September 2022, with the data for all surviving birds being right-censored at that date.

SURVIVAL MODEL SET A: SURVIVAL IN RELATION TO ORIGIN, AGE AND YEAR.

For all further survival analyses, we wished to include potential effects on DMR of various combinations of covariates. We did this within a Generalised Linear Modelling (GLM) framework, as described by Aebischer (1999). The dependent variable in all analyses was the binary outcome death (response variable = 1) or survival (response variable = 0). The assumed error distribution was binomial, so each day of monitoring is treated as a binomial trial. We used a logit link function because DMR must be within the range zero to 1. We fitted the model by a maximum-likelihood method with Laplace Approximation. Independent categorical variables were modelled as fixed effects in the GLM. We evaluated a set of 18 models (Model Set A), which included all combinations of the main effects of three independent variables, all of which were categorical variables (factors). These were the calendar year in which monitoring occurred (YEAR: a factor with five states 2017/2018, 2019, 2020, 2021, 2022), whether the bird was wild or a released captive (ORIGIN: a factor with two states), whether it was adult or subadult at release (AGE: a factor with two states). We grouped the monitoring years 2017 and 2018 together as one category in YEAR because the number of monitoring days in 2017 was small and no mortality was observed in that year. We included models with and without all possible two-way interactions between these variables. For

each of the 18 models, we calculated the small-sample Akaike Information Criterion (AIC_c) and the AIC_c weight, with the number of tagged birds (99) being used as *n* in the AIC_c calculation (Burnham & Anderson 2002). We used model-averaging of models within 2 AIC_c points of the model with the lowest AIC_c to obtain a predictive model (Burnham & Anderson 2002). We compared DMR estimates between pairs of groups of birds using Fisher Exact 2x2 tests. We used the *m* and (*d*-*m*) values for each of the two groups as the entries in the 2x2 contingency tables.

SURVIVAL MODEL SET B: SURVIVAL OF RELEASED CAPTIVE BIRDS IN RELATION TO AGE, YEAR, TIME ELAPSED SINCE RELEASE AND SEASON.

An alternative set of binomial logistic regression models was fitted for released birds only (Model Set B). The dependent binary variable was whether a monitored bird died or not (event) on a given focal day (trial), with the outcome for each day of monitoring being considered separately. This was done to allow DMR to be modelled in relation to the variable DAYS (the time elapsed between release and the focal day), which took a unique value for each day of monitoring of a given individual. There were three other independent variables in this model set: AGE, YEAR and SEASON. AGE was a factor with four states, representing an age class at the time of each focal day of monitoring. Birds released as subadults were coded '2' on release (i.e. in their second year), then '3', '4' and '5' after one, two and 3+ years post release. Birds released as adults were coded '5' throughout. YEAR was a factor with five states representing the calendar year in which the focal day of monitoring fell. SEASON was a factor with two states: summer (April-September) and winter (October-March)). This model set included models with all combinations of the main effects of the four independent variables and the null model with no explanatory variables, giving 16 models in all.

For each of the 16 models, we calculated the small-sample AIC_c and the AIC_c weight, with the number of tagged birds (99) being used as *n* in the AIC_c calculation (Burnham & Anderson 2002). We report model-averaged parameter estimates of models within $\Delta AIC \leq 2$ of the model with the lowest AIC.

GRAPHICAL ILLUSTRATION OF SURVIVORSHIP PATTERNS

We made graphical representations to illustrate the survival of tagged vultures after they were released by plotting Kaplan-Meier diagrams for each of 15 groups of birds released at the same time or close together in time (Kaplan & Meier 1958). Each group consisted of birds of the same age class at release and the same origin (wild or captive released). For nine groups, the birds were released on the same date, but for four groups, results for two groups released on dates close together in time were combined using staggered-entry Kaplan-Meier method (Pollock *et al*. 1989).

HOME RANGES OF WILD AND RELEASED GPS-TAGGED WHITE-RUMPED VULTURES

GPS positions were filtered by removing positions obtained before release and right-censoring the data at the end of the study period (8th September 2022), or when individuals died or were lost to follow-up due to tag loss / failure. Tag position data obtained after the time of death were also removed for known or suspected mortalities. We applied a spatiotemporal filter to remove spatial duplicates, those positions considered unrealistic based on reported speeds, and removed birds with too few locations to estimate realistic home range sizes (*n* = 1 bird with 5 GPS fixes). This left a total of 424,949 (mean: 4336.21, range: 176 – 17,355, *n* = 98 birds) eligible GPS locations. GPS locations. We pre-processed the data using the spatio-temporal filters implemented in the package *SDLfilter* (v. 2.2.1; Takahiro Shimada, 2022). Data were prepared and manipulated in R (R Core Team 2022) using the packages *track2KBA* (vers. 1.0.3; Beal *et al*., 2021) and *tidyverse* (v. 1.3.2; Wickham *et al*., 2019).

We split the data into four groups: wild adults (WA), wild subadults (WS), released adults (RA) and released subadults (RS), and transformed the co-ordinates of the tracks by applying a cylindrical equal-area projection (Behrmann projection) and WGS 84 datum. To minimise the geographical distortion, we defined the central meridian as the arithmetic mean of the distribution of the coordinates.

Space use was calculated using kernel density (KD) estimation, a non-parametric technique for deriving the utilization distribution (UD), which is a probability surface describing the probability of an animal occurring in space (Worton 1989). The determination of the smoothing parameter, or bandwidth, is critical as if incorrectly assigned can lead to over- or underestimation of the UD(see the examples in Beal *et al*., 2021). We used the function *findScale* from the *track2KBA* package to choose the most adequate scale for each group: RA (1.0 km), RS (0.5 km), WA (4.0 km) and WS (2.0 km) with a smaller grid for the released (0.7 km^2) than for the wild birds (3 km^2). Then we extracted the 50% and 95% isopleths from the UD as the core and home ranges of the bird, respectively.

We also calculated home range (HR) size as the 95% minimum convex polygon (MCP_{95}), to define the range of each bird, and 50% MCP (MCP_{50}) to estimate the core range. Although MCPs are often criticised for overestimating HR size through inclusion of unused areas (Huck, Davison & Roper 2008), their estimation enabled a direct comparison with the only other study of White-rumped Vulture movements (Gilbert *et al*. 2007). HR estimation was performed using the tools implemented in the package *adehabitat* (Calenge, 2006).

Inspection of model residuals for both KD and MCP estimates indicated violation of the assumption of normality and the undue influence of certain points, so we log_{10}-transformed all home range estimates. We modelled each of the transformed home range values as the dependent variable using a Generalised Linear Model with an identity link function and normal error distribution (i.e. an ordinary least squares regression model). We modelled the effects of three independent variables: DAYS, ORIGIN and AGE. DAYS was the number of monitoring days between release and loss-to-follow-up. We included this variable to allow for the possibility that the area covered by a bird increased with time. ORIGIN was a factor with two states (wild or released captive). AGE was a factor with two states (adult or subadult at release). We tested the two-way interaction between ORIGIN and AGE using the *emmeans* function in R (Lenth 2022).

Results

INITIAL COMPARISONS BETWEEN WILD AND RELEASED CAPTIVE BIRDS

We inspected the Kaplan-Meier graphs (Fig. 2) for indications of differences in patterns of survival in relation to age class, origin and time. For adult birds, there was a clear tendency for survival to be lower for released captive than for wild birds. For subadults, there was an indication that captive released birds survived less well than wild birds, but the difference was less clear-cut. The survival of wild birds appeared to be lower for subdaults than for adults, but the difference between age classes was not marked for released captive birds. There was no obvious trend in survival over time within the six-year period. Comparison of estimates of annual survival rates among age classes and between wild and released captive birds support these conclusions (Fig. 3). The annual survival rate of wild adults was higher than that of released captive adults, and their 95% confidence intervals did not overlap. The difference in annual survival between wild and released captive subadults was in the same direction but was less marked and the confidence intervals of estimates for the two origin groups overlapped. We intend this initial presentation of results to be preliminary and illustrative because they do not allow for possible confounding effects of covariates such as time period. We used the more rigorous GLM and multi-model inference approaches to examine the effects of multiple covariates in detail in the following sections.

MODEL SET A: SURVIVAL IN RELATION TO ORIGIN, AGE AND YEAR

The model with the lowest AICc value included main effects of AGE, ORIGIN and YEAR and the AGE*ORIGIN two-way interaction (Table S3). The next-best model included the main effects ORIGIN and YEAR, and this was the only model in the set with an AICc value within 2 of the best model. (Table S3). After model-averaging of these two top models, there was a significant two-way interaction between AGE and ORIGIN (Table 1). For adults, the annual survival rate of released

297 captive-reared birds was significantly lower than for wild birds (annual survival estimates: adults:
298 wild, 0.974 (95% CI, 0.910, 0.997), released captive, 0.640 (CI 0.490, 0.771); Fisher exact test, *P* =
299 0.0001; Fig. 3). For subadults, the annual survival rate of released captive-bred birds was non-
300 significantly lower than for wild birds (wild, 0.880 (CI 0.721, 0.966), captive, 0.758 (CI 0.579, 0.887);
301 Fisher exact test, *P* = 0.25; Fig 3). DMR varied among calendar years with the model-averaged effects
302 of YEAR showing that, after allowing for other variables, DMR values ranked from lowest to highest
303 as 2021 < 2017/2018 < 2022 < 2019 < 2020 (Table 1).

304 MODEL SET B: SURVIVAL OF RELEASED CAPTIVE BIRDS IN RELATION TO AGE, YEAR, TIME SINCE
305 RELEASE AND SEASON.

306 The model with the lowest AICc value included the main effects of DAYS and YEAR (Table S4). The
307 next-best model included the main effects DAYS, YEAR and SEASON, and this was the only model in
308 the set with an AICc value within 2 of the best model (Table S4). After model-averaging of these two
309 top models, there was a significant negative effect of DAYS, i.e. daily mortality declined with
310 increasing time since release (Table 2, Fig. 4). DMR varied among calendar years with the model-
311 averaged effects of YEAR showing that, after allowing for other variables, DMR values ranked from
312 lowest to highest as 2017/2018 < 2021 < 2019 < 2022 < 2020 (Table 2).

313 CAUSES OF DEATH OF GPS-TAGGED WHITE-RUMPED VULTURES

314 A total of 31 'deaths' has been recorded, of six wild and 25 released birds (Table 3), including one
315 wild bird whose tag stopped transmitting that was never seen again, nor a corpse found. The most
316 common cause of death was birds being picked up weak through starvation and dehydration and
317 taken into care (*n* = 11 released birds), although five of these birds were subsequently rehabilitated
318 and later released. The remaining six birds did not respond to efforts at rehydration and feeding and
319 died in captivity; subsequent post-mortems did not discover any other cause of death. Other major
320 causes of death included electrocution on domestic powerlines (*n* = 4 captive birds). Six birds (*n* = 2
321 wild and 4 captive) were found to be infested with roundworms, although this is unlikely to have

been the cause of death. Of the 27 birds to which a cause of death could be assigned (Table 3), there were no confirmed cases of NSAID poisoning.

The tag of one of birds that died of unknown causes stopped sending transmissions, after it had travelled > 1000 km to Himachal Pradesh, India, close to the border with Pakistan, the tag having been active for c.2.5 years. The other three birds with unknown causes of death were in a decomposed state when found, so could not be sent for post-mortem. One further wild bird, which was still alive when its tag fell off (so is not included in Table 3), subsequently died of unintentional poisoning. This was due to the use of poison baits being used to kill feral dogs in an incident which killed at least 69 vultures in April 2021, including 35 White-rumped Vultures, 31 Himalayan Griffons *Gyps himalayensis*, 2 Cinereous Vultures *Aegypius monachus* and 1 Slender-billed Vulture (SAVE 2021a).

HOME RANGES OF WILD AND RELEASED GPS-TAGGED WHITE-RUMPED VULTURES

The number of days that birds were monitored had a positive effect on estimates of both KDE_{50} and KDE_{95}, t_{93} = 3.23, P = 0.002, t_{93} = 2.70, P = 0.008, respectively). Both the 95% range (KDE_{95}, t_{93} = 19.89, P < 0.0001; MCP_{95}, t_{93} = 10.85, P < 0.0001) and 50% range (t_{93} = 23.89, P < 0.0001; MCP_{50}, t_{93} = 12.30, P < 0.0001) were significantly larger for wild compared to released birds (Table 4). This was true for both birds released as adults (*emmeans*, KDE_{95}: t_{93} = 19.89, P < 0.0001; KDE_{50}: t_{93} = 23.89, P < 0.0001; MCP_{95}, t_{93} = 10.85, P < 0.0001, MCP_{50}, t_{93} = 12.30, P < 0.0001) and subadults (KDE_{95}: t_{93} = 13.06, P < 0.0001; KDE_{50}: t_{93} = 18.79, P < 0.0001; MCP_{95}, t_{93} = 6.16, P < 0.0001, MCP_{50}, t_{93} = 7.72, P < 0.0001). KDE_{95} of released birds was significantly larger for adults (t_{93} = 3.51, P = 0.003), but not subadults (t_{93} = 2.08, P = 0.13). KDE_{50} was larger in adults for both released and wild birds (t_{93} = 6.97, P < 0.0001 and t_{93} = 4.50, P = 0.0001, respectively). There were no significant differences in either KDE_{95} or KDE_{50} or MCP_{95} or MCP_{50} between age groups in either wild or released captive birds (all pairwise comparisons, P > 0.3; Table 4).

347 *Discussion*

348 Our estimates of annual survival rates for White-rumped Vultures are the first for any South Asian
349 *Gyps* species to be derived from direct study of individually-marked birds. It is thus a test of the
350 efficacy of the bans on veterinary NSAIDs, and subsequent advocacy and education work carried out
351 by conservationists. We also provide the first estimated survival rates of birds from a reintroduced
352 population in Asia. The annual survival rate of wild GPS-tagged White-rumped Vultures was high,
353 comparable to those of other *Gyps* species, and significantly higher than that of captive birds
354 released from the conservation breeding population. The high survival rate of wild birds, and the
355 lack of evidence of NSAID poisoning from post-mortems of recovered carcasses of tagged birds,
356 suggest that the impact of diclofenac and other toxic NSAIDs in the area of Nepal occupied by the
357 tagged vultures was minimal. Hence, we suggest that this area can be considered a genuine Vulture
358 Safe Zone. Although the daily probability of released birds dying declined over time, suggesting that
359 birds were adapting to life in the wild, their overall high mortality rate raises questions regarding the
360 adequacy of the procedure for releasing birds into the wild.

361 As with other large raptors with a long period of maturation and a low reproductive output, the
362 population growth rate of vultures is more sensitive to changes in adult survival than to changes in
363 other demographic rates (Stahl & Oli 2006). Across species, survival rates of raptors tend to increase
364 with increasing body mass (Newton *et al*. 2016), with adult survival of *Gyps* vultures being very high,
365 e.g. 96.8% in wild Eurasian Griffons *Gyps fulvus* in Spain (Arrondo *et al*. 2020) and 99.9% for White-
366 backed Vultures *G. africanus* in South Africa (Monadjem *et al*. 2012). Juveniles, as with most other
367 species, tend to have lower annual survival rates, e.g. 85.8% for wild-born young Eurasian Griffons in
368 France (Sarrazin *et al*. 1994), and 85.2 – 89.1% for 2-4-year-old immature White-backed Vultures
369 (Monadjem *et al*. 2012). Our figures for the survival of wild adult and subadult White-rumped
370 Vultures (97.4% and 88.0%, respectively) are similar, suggesting that the environment over which
371 the tagged birds ranged was not strongly affected by any additional mortality caused by

anthropogenic factors, such as toxic NSAIDs, setting of poison baits to kill carnivores, electrocution, or collisions with built structures. None of the 50 wild tagged birds were recorded as having died from any of these anthropogenic causes during the five years they were being monitored.

The high survival of wild-origin birds in Nepal contrasts with the situation in India at the height of the vulture crisis in the early 2000s, when White-rumped vultures were suffering 40-50% annual mortality from diclofenac poisoning alone (Green *et al*. 2004). Further support for the view that additional mortality caused by diclofenac is low in this part of Nepal is provided by the results of undercover pharmacy surveys, which found that diclofenac ceased to be offered for veterinary use, especially in the western lowlands, where the tagged vultures ranged (Galligan *et al*. 2021), and that it was largely replaced by the vulture-safe NSAID meloxicam. None of 27 tagged birds to which a cause of death could be assigned died from NSAID poisoning.

Long-term monitoring of White-rumped and Slender-billed Vultures in Nepal by road transect surveys indicates that trends in populations of both species changed from decline to increase in about 2012 (Galligan *et al*. 2020), which is when undercover pharmacy surveys indicate that availability of diclofenac fell to a very low level (Galligan *et al*. 2021). The population growth rates of both species during the recent increase (21.7% and 41.3% per annum for White-rumped and Slender-billed Vultures, respectively), estimated from the road transect data, was approximately as rapid as is possible for *Gyps* vultures under the most favourable conditions, given the low maximum fecundity rate (Galligan *et al*. 2020). Taken together, these estimates of a marked change in population trend and our new estimates of recent high survival of wild-origin vultures suggest that conditions in Nepal have become favourable for vultures and conducive to the recovery of their populations in recent years.

This is not to say that there are no remaining anthropogenic threats to vultures in Nepal. There are known to be vulture-toxic NSAIDs other than diclofenac in use, such as nimesulide (Cuthbert *et al*. 2015, Galligan *et al*. 2021, Nambirajan *et al*. 2021). Deliberate setting of poison baits to kill

carnivores has been observed to kill vultures in Nepal, including one tagged bird several months after its tag had fallen off (SAVE 2021a). Electrocution on power infrastructure also occurs and sometimes affects wild vultures (Chaudhary *et al*. 2019). However, all these hazards currently appear to be at a sufficiently low level to permit population growth, and actions to counter them can be incorporated into VSZ conservation advocacy.

Carcasses of four of the 31 tagged birds which died were not retrieved or not found quickly enough for a post-mortem to be performed. This introduces uncertainty into the attribution of causes of death. Future programmes of GPS tagging, in Asia and elsewhere, will need to ensure that dedicated teams of surveyors are in place and able to respond quickly to successfully retrieve carcasses of any vultures that die, within 1-2 days of death, so that post-mortems and collection of fresh tissue samples can be carried out to identify causes of death.

An aspiration for reintroduction programmes is that released birds have comparable survival rates and behaviour to those of wild birds. Annual survival rates of reintroduced *Gyps* vultures can be high and often comparable to those of wild-born birds, e.g. Eurasian Griffon, 91.5% in Italy (Monti *et al*. 2023), 95.5% in Sardinia (Berlinguer 2019), 98.7% and 96.7% for adults in France (Sarrazin *et al*. 1994, Le Gouar *et al*. 2008), although birds released as juveniles / immatures survived less well, e.g. 75.5% (Sarrazin *et al*. 1994). In our study, annual survival of released White-rumped Vultures was relatively low (64.4% and 75.8% for adults and subadults, respectively). Whereas higher mortality can be expected in subadult birds, due to inexperience and lower competitive ability (Bose & Sarrazin 2007), low survival rates in White-rumped Vultures released as adults may suggest an effect of the time spent in captivity. Although such 'release effects' may not be unusual, e.g. adult Eurasian Griffons in France experienced low (74.3%) survival rates in the first year after release (Sarrazin *et al*. 1994), those birds released as adults in Nepal had been taken into captivity as chicks up to a decade or more beforehand. Although it may be generally advantageous to release adults (Sarrazin & Legendre 2000), the length of time these birds spent in captivity may have made them ill-equipped

to adapt to life in the wild, although the probability of survival of released birds tended to increase with increasing time since release, suggesting they were becoming better adapted to life in the wild, as found elsewhere (Efrat *et al*. 2020).

Home ranges of vultures can be huge, often crossing national boundaries, as birds search for often unpredictable sources of food. However, our estimates are smaller than those of three species of *Gyps* vultures in Africa (KDE_{95}; 23,649 km^2 (White-backed Vulture) to 172,450 km^2 (Rüppell's Vulture *G. ruppellii;* Kane *et al*. 2022), and in a previous study of five White-rumped Vultures in Pakistan (MCP_{95}; 10,225 v 24,154 km^2; Gilbert *et al*. 2007). Variation in home range size in the Pakistan study was attributed to the differing provision of supplementary food, with movements more restricted when birds were regularly feeding at a vulture restaurant (Gilbert *et al*. 2007). Although vulture restaurants do not always result in smaller movements (Kane *et al*. 2016), the individual variation observed in our study was probably also due to differing reliance on the Vulture Restaurant located at the release site, and the location of an individual's breeding colony (several tagged birds nested within 5 km of the feeding site). The availability of supplementary food may also explain the similarity in home range size of adults and immatures, whereas in other studies, immatures often range over larger areas (Kane *et al*. 2022). The impact of the vulture restaurant at the release site was most obvious in the comparison of wild and released birds' home ranges, with the former being 1-2 orders of magnitude larger (Table 4). However, despite the above differences between wild and released birds, the latter have begun to assimilate into the local wild population, with several birds already successfully breeding in the local area (SAVE 2022).

The biggest source of mortality for released birds was being picked up weak through dehydration and starvation, often after unusually long flights. This was a particular issue in 2020, when six birds were recovered and taken into care. Such long flights (up to 350 km from the feeding site) were unknown prior to March 2020. We speculate that the closure of two local slaughterhouses because of Covid-19 restrictions forced wild birds to travel further in search of food (K. Bhusal, pers. comm),

with some of the released birds joining them, undertaking journeys for which they may not have been physically ready. The slaughterhouses have since reopened, and there have been no further long flights undertaken by released birds.

Following concerns relating to post-release survival, certain measures were implemented to address the potential issues experienced by released birds. These included extending the holding aviary (to 30 m length) to improve birds' flight capabilities (see above), although such training was stopped due to the risk of injury to the birds, and improving hygiene measures at the feeding site to reduce the risk of disease (Supplementary Information, Appendix A). Since these hygiene measures have been taken, there have been no further cases of heavy roundworm infestation.

Based on the high survival rate of wild GPS-tagged vultures, the absence of NSAID-poisoning, along with the previous removal of veterinary diclofenac from pharmacies (Galligan *et al*. 2021), and the partial recovery of vulture populations (Galligan *et al.* 2020), the Nepal VSZ was declared officially safe – the world's first genuinely safe VSZ - by the Technical Advisory Committee of the Saving Asia's Vultures from Extinction (SAVE) consortium in December 2021 (SAVE 2021b).

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Conflict of Interest Statement

The authors declare that they have no known conflicts of interest that could have appeared to influence the work reported in this paper.

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641 **SUPPLEMENTARY INFORMATION**

642 APPENDIX A: Tables S1-S4

643 APPENDIX B: Nepal Release Protocol

Table 1. Model-averaged parameter estimates for the two best models in Model Set A (see Table S3) of the Daily Mortality Rate of White-rumped Vultures in relation to age class (subadult (S), adult), origin (wild (W) or released), year and the ORIGIN*AGE two-way interaction. Except for the intercept term, the parameter values shown are model-averaged differences in logit(DMR) between the reference value (intercept) for released captive adults in 2017/2018 and each of the other classes or interactions.

Parameter	Estimate	SE	z	*P*
Intercept	-7.536	0.723	10.38	< 0.0001
Age (S)	-0.591	0.435	1.35	0.18
Origin (W)	-2.506	0.805	3.11	0.002
Year (2019)	0.723	0.821	0.88	0.38
" (2020)	1.546	0.761	2.02	0.04
" (2021)	-0.334	1.000	0.33	0.74
" (2022)	0.717	0.803	0.89	0.37
Origin (W)*Age(S)	2.114	0.968	2.17	0.03

Table 2. Model-averaged parameter estimates from the top two logistic regression models (see Table S4) of the daily survival of released captive White-rumped Vultures in relation to days since release, year, and season.

Parameter	Estimate	SE	z	*P*
Intercept	-7.796	1.026	7.60	< 0.0001
Days	-0.002	0.001	2.12	0.03
Year (2019)	1.521	1.084	1.40	0.16
" (2020)	2.314	1.059	2.19	0.03
" (2021)	0.472	1.456	0.32	0.75
" (2022)	1.659	1.093	1.52	0.13
Season (W)	-0.381	0.420	0.91	0.36

Table 3. Probable causes of death of tagged wild and released captive White-rumped Vultures *Gyps bengalensis*. The figures do not include two wild birds with tags which stopped transmitting and were not located.

	Cause of death							
Bird	Predation	Picked up weak	Persecution	Electrocution	Collision	Starvation	Unknown	Unknown - roundworm
Wild	0	0	0	0	0	1	3	2
Captive	2	11	1	4	2		1	4

Table 4. Mean, minimum and maximum number of days over which White-rumped Vultures GPS-tagged at Kawasoti, Nawalparasi District, Nepal between 2017 and 2021 were monitored, and 50% and 95% kernel density estimate and Minimum Convex Polygon home ranges (km^2). Birds are grouped according to their origin (wild or released) and age at tagging / release (adult or subadult).

		Birds	Days			km^2				km^2			
Origin	Age	N	N	Min	Max	kde_50	SD	kde_95	SD	mcp_50	SD	mcp_95	SD
Wild	Adult	35	799.40	175	1975	246.07	225.79	3653.82	2758.25	1741.71	2332.44	10225.69	23111.38
Wild	Subadult	15	763.87	158	1462	137.97	200.01	2568.71	2114.32	2356.44	2759.98	8520.13	6875.47
Released	Adult	34	409.82	13	1764	5.24	6.33	83.77	271.10	221.60	1069.45	912.25	2610.01
Released	Subadult	15	703.00	47	1452	1.22	0.38	20.49	23.45	3.87	8.23	338.47	784.57

Figure legends

Figure 1. A summary of the movements of wild (blue) and released captive (red) GPS-tagged White-rumped Vultures, tagged between 2017 and 2021 at Kawasoti, Nawalparasi District, Nepal, separated by age at release (adults / subadults). Tagging location / release site indicated by star.

Figure 2. Kaplan-Meier diagrams showing the proportions of monitored groups of tagged adult (upper panel) and subadult (lower panel) White-rumped Vultures still known to be alive in relation to date. Each line relates to a group of vultures released to the same time, except for four cases where data for two groups released close together in time were combined (see text). Numbers at the left-hand end of each line show the initial number of birds alive in the group. Results for wild birds are shown in blue and those for released captive birds are shown in red. Vertical grey lines show calendar years.

Figure 3. Annual survival rates of White-rumped Vultures *Gyps bengalensis*, GPS-tagged at Kawasoti, Nawalparasi District, Nepal, from 2017 to 2022. Vertical lines show 95% confidence intervals.

Figure 4. Daily probability of a released captive GPS-tagged White-rumped Vulture dying with respect to the number of days since it was released. Black line shows predicted relationship from model-averaged GLM of two top models (see Table 2), grey lines show standard errors. To model the relationship, the other parameters were held constant: AGE = '2' (second-year), YEAR = '2020', SEASON = 'Summer'.